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Cite as: AIP Conference Proceedings **1895**, 050003 (2017); https://doi.org/10.1063/1.5007375
Published Online: 12 October 2017

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Analysis of Stochastic Phenomena in Ricker-type Population Model with Delay

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Abstract. A phenomenon of the noise-induced extinction is studied on the base of the conceptual Ricker-type model with the delay and Allee effect. This nonlinear discrete population model exhibits the persistence with the different form of attractors, both regular and chaotic. For this model, the persistence zones are defined by points of the crisis bifurcations. The phenomenon of the noise-induced extinction is investigated with the help of direct numerical simulations and by the semi-analytical new method based on the stochastic sensitivity functions. In the stochastic analysis, a geometrical approach taking into account a mutual arrangement of the confidence domains and basins of attraction is used.

INTRODUCTION

It is well known that nonlinear population systems can exhibit complex dynamic regimes, both regular and chaotic [1, 2]. The deterministic theory of the population dynamics is well developed and based on the mathematical theory of bifurcations. At present, the challenging problem is the study of the nonlinear phenomena in stochastic population models [3, 4, 5, 6]. Here, a phenomenon of the noise-induced extinction is one of the most attractive [7, 8]. The extinction regimes in population systems are often attributed to the Allee effect [9, 10]. The Allee effect implies the existence of a threshold population level below which the population goes to the extinction. The stochastic population systems with Allee effect were studied in [11, 12].

In the theory of the discrete-time population models, Ricker-type systems are well-known [13, 14]. The Ricker-type models with delay were studied in [15]. In the present paper, we study the noise-induced extinction in the Ricker model combining both Allee effect and delay. Even in the deterministic case, this model exhibits a wide diversity of attractors and bifurcations.

The full mathematical description of the stochastic dynamics in discrete systems, is given by the Frobenius-Perron equations [16]. However, a direct use of these functional equations is very difficult technically, even in one-dimensional case. For the constructive description of probabilistic distributions near deterministic attractors the new method based on the stochastic sensitivity functions technique [17, 18, 19] was proposed. In the present paper, we apply this technique to the analysis of noise-induced extinction in the Ricker model with delay and Allee effect.

We present a short description of main properties the deterministic version of the considered model. For the stochastically forced model, the phenomenon of the noise-induced extinction is studied. The analysis of this phenomenon is based on the stochastic sensitivity functions technique and confidence domains method. For the investigation of the noise-induced extinction, a geometrical approach taking into account a mutual arrangement of the confidence domains and basins of attraction is used.

DETERMINISTIC MODEL

An initial well-known Ricker model is defined by the one-dimensional discrete-time system

$$x_{t+1} = x_t e^{\mu(1-x_t)},$$

Application of Mathematics in Technical and Natural Sciences
AIP Conf. Proc. 1895, 050003-1–050003-7; https://doi.org/10.1063/1.5007375
Published by AIP Publishing. 978-0-7354-1579-9/$30.00

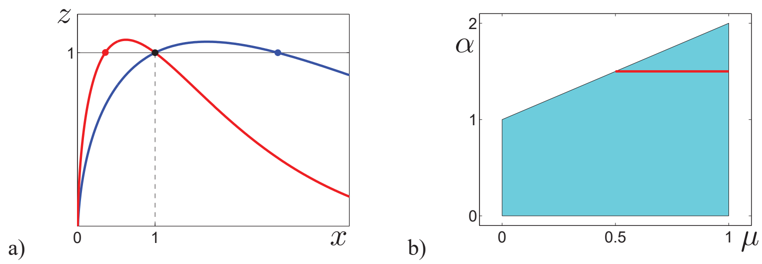

FIGURE 1. Deterministic model: a) plots of the function $z = g(x)$ for $1 < \alpha < \mu + 1$ (red curve), and $\alpha > \mu + 1$ (blue curve); b) stability domain of the equilibrium M_1 (red line for $\alpha = 1.5$)

where x_t is the population size at the time t, and the parameter $\mu > 0$ is an intrinsic growth rate. Consider a modification of this population model with the embedded delay and Allee effect

$$x_{t+1} = x_t^\alpha e^{\mu(1-x_{t-1})}. \tag{1}$$

In the model (1), and the coefficient $\alpha \geq 1$ is a tuning parameter that regulates a strength of the Allee effect.

Eq. (1) with delay can be rewritten in the form of the two-dimensional system without delay

$$\begin{aligned} x_{t+1} &= x_t^\alpha e^{\mu(1-y_t)} \\ y_{t+1} &= x_t. \end{aligned} \tag{2}$$

For $\alpha = 1$, the system (2) has no the Allee effect. In this case, the system (2) has two equilibria $M_0(0,0)$ and $M_1(1,1)$. The equilibrium M_0 is unstable for any μ, and M_1 is stable for $0 < \mu < 1$. At $\mu = 1$, the system passes the Neimark-Sacker bifurcation. For $\mu > 1$, in system (2), different type attractors (closed invariant curves, discrete cycles, chaos) are observed. The basin of attraction of these attractors is $\{(x,y) | \, x > 0, y \geq 0\}$.

Consider now how the embedded Allee effect changes the dynamics of the system. For $\alpha > 1$, the deterministic system (2) has three equilibria: $M_0(0,0)$, $M_1(1,1)$, and $M_2(\bar{x}_2, \bar{y}_2)$. Coordinates $\bar{x}_1 = \bar{y}_1 = 1$ of the equilibrium M_1, and coordinates $\bar{x}_2 = \bar{y}_2$ of the equilibrium M_2 satisfy the following equation:

$$g(x) = x^{\alpha-1} e^{\mu(1-x)} = 1.$$

A mutual arrangement of $\bar{x}_1 = 1$ and $\bar{x}_2$ depends on the sign of the derivative $g'(1) = \alpha - \mu - 1$. In the illustrative Figure 1a, two specific cases are shown. Here, the function $z = g(x)$ is plotted for $1 < \alpha < \mu + 1$ (red curve), and $\alpha > \mu + 1$ (blue curve). The black dot marks the position of $\bar{x}_1 = 1$, and red and blue dots show the position of $\bar{x}_2$ in these two cases. For $1 < \alpha < \mu + 1$, we have $0 < \bar{x}_2 < \bar{x}_1$, and for $\alpha > \mu + 1$, we have $\bar{x}_2 > \bar{x}_1$.

In contrast to the case without Allee effect, the equilibrium M_0 is stable for any $\alpha > 1$. The equilibrium M_1 is stable for $-1 + \alpha < \mu < 1$. The stability region for the equilibrium M_1 is shown in Figure 1b. When α increases and approaches $\alpha_* = 2$, the μ-interval $(-1 + \alpha, 1)$ of the stability of the equilibrium M_1 contracts and vanishes.

In the current paper, we fix $\alpha = 1.5$. The corresponding μ-interval $(0.5, 1)$ of the stability of the equilibrium M_1 is shown by red in Figure 1b. In Figure 2, the bifurcation diagram of system (2) with $\alpha = 1.5$ is presented. Here, x-coordinates of the equilibria are plotted by solid and dashed lines in zones where these equilibria are stable or unstable, respectively. At $\mu_* = 0.5$, an interchange of the stability between equilibria M_1 and M_2 occurs. For $\mu = 1$, the Jacobi matrix at the point M_1 possesses a pair of complex eigenvalues $\frac{\alpha}{2} \pm \sqrt{1 - \frac{\alpha^2}{4}}\, i$ with the unit modulus. When the parameter μ passes the value $\mu = 1$, the equilibrium M_1 loses its stability, and the deterministic system exhibits the Neimark-Sacker bifurcation. As a result of this bifurcation, the closed invariant curve is born.

For $\mu > 1$, in system (2), regular (closed invariant curves and discrete cycles) and chaotic attractors are observed similar to the case $\alpha = 1$ without Allee effect. However, in the system with the Allee effect, there is a new essential feature: with increasing μ, the tree of nontrivial attractors expands, touches the unstable equilibrium, and disappears as a result of the crisis bifurcation (see Figure 2). An analogous scenario is observed under decreasing μ to the left from the point μ_*. Let us denote by μ_1 the left crisis bifurcation point, and by μ_2 the right crisis bifurcation point. For $\alpha = 1.5$, the crisis bifurcation points are $\mu_1 = 0.1285$, $\mu_2 = 1.277$.

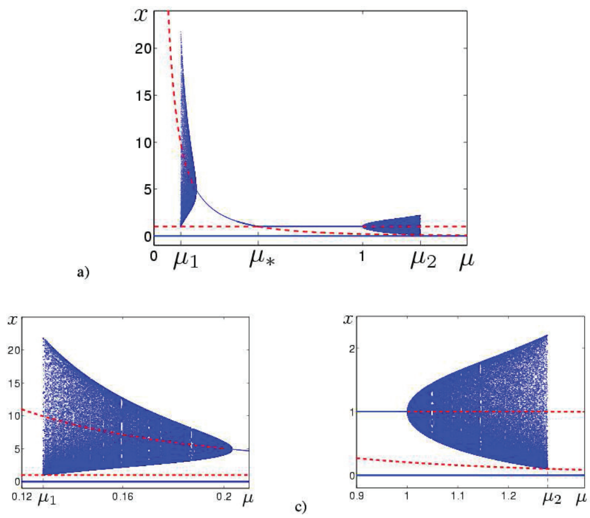

FIGURE 2. Bifurcation diagram for $\alpha = 1.5$ (a) with the enlarged fragments (b), (c). Here, $\mu_1 = 0.1285$, $m_2 = 1.277$, $\mu_* = 0.5$

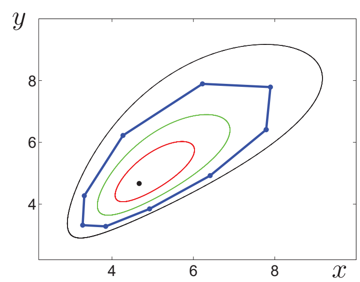

FIGURE 3. Attractors of the deterministic system (1) with $\alpha = 1.5$: $\mu = 0.18$ (black); $\mu = 0.1872$ (blue); $\mu = 0.195$ (green); $\mu = 0.2$ (red); $\mu = 0.21$ (black dot)

So, the system (2) with Allee effect is bistable in the interval $0 < \mu_1 < \mu < \mu_2$, and monostable otherwise. In the zone of the bistability, the trivial stable equilibrium M_0 coexists with the nontrivial attractors, both regular and chaotic. Here, a dynamics of the system depends on the initial point. If the initial point of the trajectory belongs to the basin of attraction of the trivial equilibrium M_0, then the trajectory tends to M_0, and the population is extinct. If the initial point lies in the basin of attraction of the nontrivial attractor, then the regime of the population existence depends on $\mu \in (\mu_1, \mu_2)$. The population can persist in the form of the equilibrium, periodic, quasiperiodic, or chaotic oscillations.

When the system (2) is monostable ($\mu \in (0, \mu_1) \cup (\mu_2, \infty)$), all solutions tend to zero (population is extinct) independently of the initial data. So, in the system with the Allee effect, a survival zone is (μ_1, μ_2). Note that for $\alpha = 1$ (system without Allee effect), the survival zone $(0, \infty)$ is unrestricted. So, we can conclude that the Allee effect contracts the persistence zone. When α tends to 2, the survival zone collapses. For $\alpha \geq 2$, the system has the only trivial attractor M_0, so the population is extinct for any initial data and any $\mu > 0$.

As one can see in Figure 2, where the enlarged fragments of the bifurcation diagram of the deterministic system are shown, two trees of attractors lying to the left and right from the point $\mu_* = 0.5$, are rather similar. In this paper we will focus on the study of the behavior of the system in dependence on the parameter $\mu < \mu_*$.

Typical examples of the nontrivial attractors are plotted in Figure 3. Here, one can see the equilibrium M_2 that is stable for $0.2032 < \mu < 0.5$, stable invariant curves for $\mu = 0.18$, $\mu = 0.195$, $\mu = 0.2$, and discrete 9-cycle for $\mu = 0.1872$.

STOCHASTIC MODEL

For the study of the influence of random disturbances on the population dynamics, we will consider the following stochastic model with the multiplicative environmental noise

$$\begin{aligned} x_{t+1} &= x_t^{\alpha} e^{\mu(1-y_t)} + \varepsilon x_t \xi_t \\ y_{t+1} &= x_t. \end{aligned} \tag{3}$$

Here, ξ_t is a standard uncorrelated scalar random process with parameters $E(\xi_t) = 0$, $E(\xi_t^2) = 1$, ε is the noise intensity.

In order to preserve the biological sense, we assume the following. If the system (3) gives $x_k \leq 0$ at some step k, then the population is extinct: $x_{k+i} = 0,\ i = 0, 1, 2, \ldots$.

Under the small random disturbances, a stochastic trajectory slightly deviates from the deterministic attractor, and forms some distribution with the random states which belong to the corresponding basin of attraction. When the noise increases, the dispersion of random states grows, and the trajectory can cross the separatrix and fall into the basin of attraction of the trivial equilibrium M_0. This means that with a high probability the solution tends to M_0. So, the population becomes extinct.

Analysing the noise-induced extinction, one has to take into account the following factors. The noise intensity is first factor. The second factor is connected with the arrangement of the basins of attraction of the trivial (equilibrium M_0) and non-trivial attractors. Here, the distance between the deterministic non-trivial attractor and a border of its basin of attraction plays an important role. The third factor is connected with the sensitivity of this attractor to the random noise.

In the parametric analysis of the phenomenon of the noise-induced extinction, we will use an analytical approach based on the stochastic sensitivity function technique and the confidence domains method [17, 18, 19].

At first, consider how this approach can be applied to the analysis of the dispersion of random states around the equilibrium $M_2(\bar{x}_2, \bar{y}_2)$, with $\bar{x}_2 = \bar{y}_2$. The stochastic sensitivity matrix W of this stable equilibrium can be expressed via $\bar{x}_2$ analytically:

$$W = \frac{\bar{x}_2^2}{(1+\mu\bar{x}_2)(1-\alpha^2-\mu^2\bar{x}_2^2)+2\alpha^2\mu\bar{x}_2} \begin{pmatrix} 1+\mu\bar{x}_2 & \alpha \\ \alpha & 1+\mu\bar{x}_2 \end{pmatrix}.$$

Eigenvalues $\lambda_{1,2}(\mu)$ for $\alpha = 1.5$ in the zone $0.2032 < \mu < 0.5$ are plotted in Figure 4. As can be seen, the stochastic

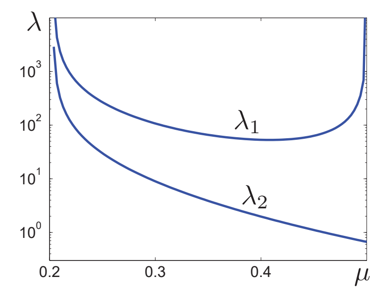

FIGURE 4. Eigenvalues $\lambda_1(\mu)$, $\lambda_2(\mu)$ of the stochastic sensitivity matrix for the equilibrium M_2 for $\alpha = 1.5$

sensitivity of the equilibrium unlimitedly increases near bifurcation points. Note that corresponding eigenvectors $v_{1,2} = (1, \pm 1)^\top$ of the matrix W do not depend on the parameter μ. The values $\lambda_{1,2}$ define sizes of semi-axes, and $v_{1,2}$ define directions of these axes for the confidence ellipse around the equilibrium M_2

$$\frac{z_1^2}{\lambda_1} + \frac{z_2^2}{\lambda_2} = 2k^2\varepsilon^2.$$

Here, $z_1,\ z_2$ are coordinates of the confidence ellipse in the basis of the normalized eigenvectors $v_{1,2}$, and ε is a noise intensity, $k^2 = -\ln(1-P)$, P is a fiducial probability.

ANALYSIS OF THE NOISE-INDUCED EXTINCTION

In the parametric analysis of the noise-induced extinction, we will study a mutual arrangement of the confidence domains and basins of attraction.

In Figures 5-7, for $\mu = 0.25$, $\mu = 0.3$, and $\mu = 0.45$, basins of attraction of the trivial equilibrium M_0 are shown by the light blue color, the basins of attraction of the equilibrium M_2 (green dot) are plotted by white, confidence ellipses are shown by red, and random trajectories are plotted by black.

In Figure 5a, for the small noise $\varepsilon = 0.05$, the confidence ellipse entirely belongs to the basin of attraction of M_2. This ellipse embraces random states of system (3), and the population exhibits small-amplitude stochastic oscillations around the equilibrium value $\bar{x} = 3.513$.

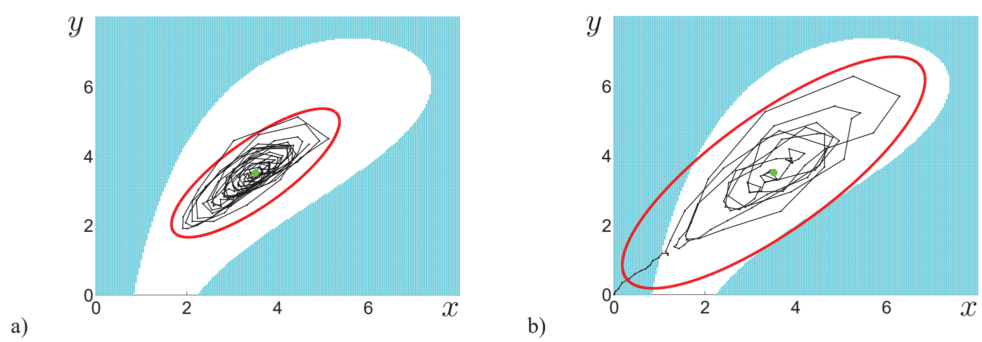

FIGURE 5. The basin of attraction of M_0 (light blue) for $\mu = 0.25$, $\alpha = 1.5$, stable equilibrium M_2 (green dot), and confidence ellipses (red) for a) $\varepsilon = 0.05$; b) $\varepsilon = 0.09$

As the noise intensity increases, the ellipse expands, crosses the separatrix which divides basins of attraction of M_2 and M_0, and starts to occupy the extinction zone. This means that with a high probability, the trajectory escapes from the basin of attraction of M_2, falls into the basin of attraction of M_0 corresponding to the extinction, and tends to M_0. In Figure 5b, the confidence ellipse for $\varepsilon = 0.09$, and the stochastic trajectory which starts at M_2 are shown.

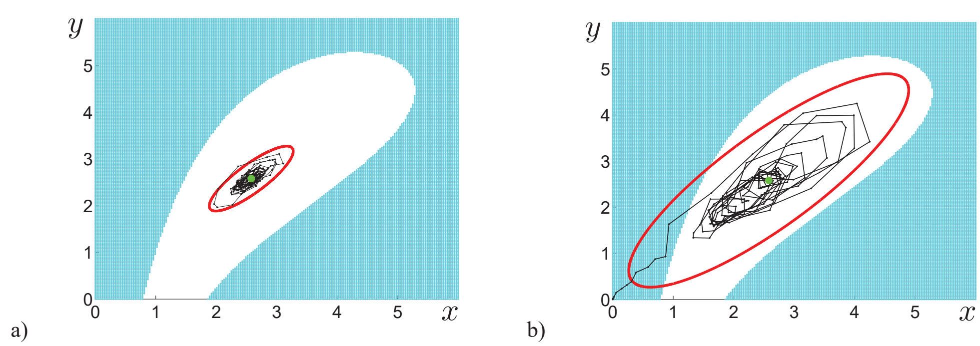

FIGURE 6. Basin of attraction of M_0 (light blue) for $\mu = 0.3$, $\alpha = 1.5$, stable equilibrium M_2 (green dot) and confidence ellipse (red) for a) $\varepsilon = 0.03$; b) $\varepsilon = 0.1$

A similar scenario of the noise-induced extinction is shown in Figure 6 for $\mu = 0.3$, and in Figure 7 for $\mu = 0.45$.

As one can see, an arrangement of the basins of attraction essentially depends on the parameter μ. Configurational peculiarities of the confidence ellipses are defined by the stochastic sensitivity of the equilibrium M_2, and the noise intensity. The Figures 5-7 well illustrate the idea that the mutual arrangement of the basins of attraction, and confidence ellipses can be effectively used in the parametric analysis of the noise-induced extinction.

A analogous approach can be used in the case when the unforced deterministic model exhibits periodic or quasi-periodic oscillations with the attractors in a form of the discrete cycle or closed invariant curve.

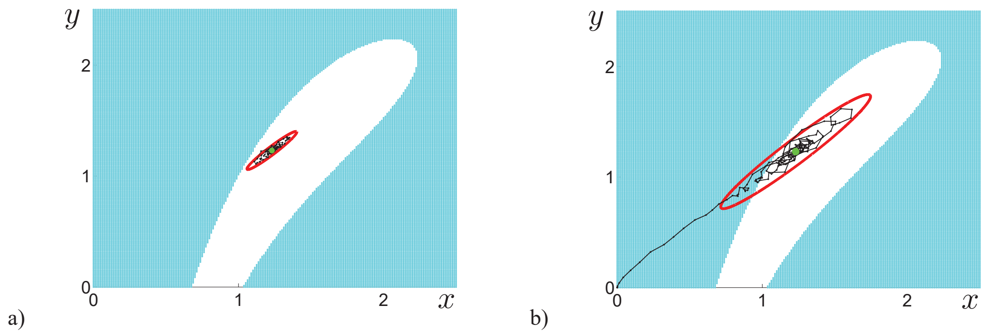

FIGURE 7. Basin of attraction of M_0 (light blue) for $\mu = 0.45$, $\alpha = 1.5$, stable equilibrium M_2 (green dot) and confidence ellipse (red) for a) $\varepsilon = 0.01$; b) $\varepsilon = 0.03$

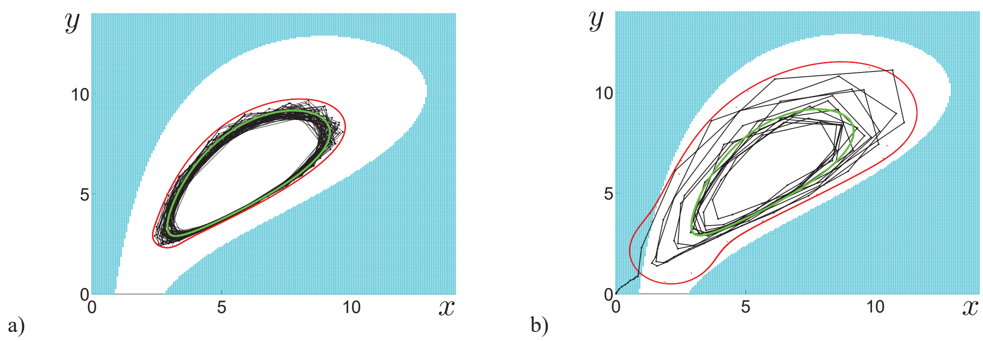

FIGURE 8. Basin of attraction of M_0 (light blue) for $\mu = 0.18$, $\alpha = 1.5$, closed invariant curve (green curve), and the external border of the confidence band (red curve) for a) $\varepsilon = 0.01$; b) $\varepsilon = 0.04$

In Figure 8, it is illustrated for $\mu = 0.18$ for the case of the closed invariant curve (green color). Here, basins of attraction of M_0 and the closed invariant curve are shown by light blue and white, respectively. By red shown is an external border of the confidence band around the closed invariant curve.

For $\varepsilon = 0.01$, the confidence band and random states belong to the basin of attraction of the closed invariant curve (see Figure 8a). The population system exhibits stochastic oscillations with small deviations from the unforced invariant curve.

For the stronger noise ($\varepsilon = 0.04$), the confidence band intersects the separatrix between basins of attraction, and stochastic trajectories with a high probability jump over the separatrix, fall into the extinction zone, and continue to move to the equilibrium M_0. So, the population becomes extinct.

CONCLUSION

In the population dynamics, the age structure and the Allee effect play an important role. To study the noise-induced extinction, we used a discrete Ricker-type system with the Allee effect and delay. One of the attractors of this model is the trivial equilibrium associated with the extinction. The other attractor corresponds to the persistence, and exists in the form of the equilibrium, discrete cycle, closed invariant curve, or chaotic attractor. The borders of the persistence zones are defined by crisis bifurcations. We studied the noise-induced extinction with the help of the stochastic sensitivity functions technique. It was shown how mechanisms of this stochastic phenomenon can be clarified and studied by the analysis of the mutual arrangement of the basins of attraction and confidence domains constructed on the base of the stochastic sensitivity functions technique. This technique is quite universal, and covers various types of attractors including a little-explored case of closed invariant curves.

ACKNOWLEDGEMENTS

The work was supported by Russian Science Foundation (grant No 16-11-10098).

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